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THE FORMATION OF MECHANICAL TISSUE IN THE TENDRILS OF PASSIFLORA CAERULEA AS INFLUENCED BY TENSION AND CONTACT

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(WITH THREE FIGURES)

Introduction

The mechanical theory of growth, as put forth by SACHS (**20**), has of late years been replaced by the idea of self-regulation in the plant depending upon external stimulus. This idea is followed quite closely by PFEFFER (**18**).[1] As a consequence, considerable attention has been directed to the effect of strain upon plant tissues, since by this new theory we might expect the plant to respond to a state of strain by a greater development of strengthening tissues. The present investigation was undertaken to determine if such self-regulation is present in the tendril that stronger mechanical tissues are produced where needed. To state the problem of the present paper: Do tendrils which are functioning to support the plant possess greater strength than those which have grasped no support, and if so, how is this strength increased, and is it due to tension or to contact, or to a combination of both?

DARWIN (**5**) observed that tendrils which have grasped no support soon die; WORGITZKY (**26**, p. 39) noted a greater breaking strength of tendrils with a support over those without. Otherwise, no attempt has been made to answer this question.

[1] For a discussion of these two theories see NEWCOMBE (**15**).

Historical

The first observations to determine the effect of strain upon the plant were by KNIGHT (12) in 1803, when he allowed fruit trees to sway in the wind in one plane only and obtained a greater increase in wood on the two sides in the direction of swaying; this he considered to be due to a greater movement of sap through a loosening of the cells, a merely mechanical process.

In 1879 BARANETSKY (2), investigating the periodicity of growth, found that when a small amount of tension (10–30 grams) was applied to a stem, it had the effect of retarding the growth in length.

SCHOLTZ (21) confirmed these observations, but found that two results were produced: first an acceleration and later a retardation of growth; the first result he attributes to a rapid growth of the cell-membrane, the second to a pathological condition in which the building up of the materials is hindered.

HEGLER (8), working along the same lines, found that this retardation of growth bears a close relation to the daily periodicity in elongation of the stem. This, he says, demonstrates that tension calls forth a response in the cell, hence is a true irritation stimulus.

HEGLER (9) also investigated the effect of tension upon the anatomical structure of stems. By gradually increasing tension on seedlings of various plants, he found that the breaking strength was in many cases nearly doubled in three days, due to an increase in amount of the collenchyma, sclerenchyma, and bast, a much greater increase than takes place under normal conditions.

BALL (1) later repeated HEGLER'S work and found no increase in mechanical tissues even in the plants with which HEGLER worked.

HIBBARD (10), also working along the same lines, found no increase in mechanical tissues with tension except in one plant (*Vinca*), where a slight increase was noted.

The work of VÖCHTING (23) upon *Helianthus annuus*, of WIEDERSHEIM (25) upon woody stems, and of KELLER (11) upon fruit stalks has likewise shown no response due to tension.

Later work by BORDNER (3) seems to show an actual increase in breaking strength and in amount of mechanical tissue in the several species with which he worked. This investigator, by the

use of a large number of individuals in each experiment, has, we believe, demonstrated that there is an actual response of the plant to tension, by which stronger tissues are laid down and the tensile strength of the part under tension increased, though not to such an extent as HEGLER's results seem to show.

Another line of investigation on the effect of tension has been followed in a comparison of the cells on opposite sides of a stem which has been prevented, by weighting, from responding to a heliotropic or negative geotropic stimulus (BALL **1**, pp. 326 f.). In this case a thickening of cell walls occurs on the convex or upper side of the stem, which has been believed by some to be due to a state of tension. A similar thickening occurs (BALL **1**, p. 339) on the upper side of a stem in a plaster cast placed horizontally, also in the concave portion of a stem which has formed a curve. In the last case cited, BALL demonstrated that no increase in breaking strength of the stem took place, a fact which he attributes to the concave side being built up at the expense of the convex side. This is substantiated by the investigations of PENNINGTON (**16**) on the effect of compression on plant stems, where he finds a reduction in the thickness of cell walls due to compression.

While a number of investigators have thus studied the effect of mechanical strain upon tissues in stems, the investigations on tendrils have been almost exclusively for the explanation of external movements, such as the cause of coiling, etc. (For explanation of external phenomena see FITTING **7**, DEVRIES **6**, and MACDOUGAL **13**.) The anatomical structure has been worked out in a comparative manner by MÜLLER (**14**) and WORGITZKY (**26**), but only by the latter writer was the tendril treated in relation to its function.

DARWIN (**5**, p. 58) noted that in petiole climbers the petioles are thickened from contact, and TREUB (**22**, p. 65) found marked changes in the anatomical structure of the portion of the petiole in contact, consisting in a greater development of the mechanical system, which is borne out in a general way by the later work of VON DERSCHAU (**24**).

MÜLLER (**14**), in his study of the tendrils of the Cucurbitaceae, found that contact produced earlier and greater lignification of sclerenchyma in the free portion on the under side (p. 127).

WORGITZKY (**26**) is the only investigator who tested the breaking strength of tendrils with and without a support. He noted that a *Passiflora* tendril which had grasped a support broke at 600 grams, while one free from a support broke at 350 grams. A tendril of *Cucurbita Pepo* likewise seemed to show greater strength of tissues when a support had been grasped. Even supposing that these tendrils tested were of the same age (which is not stated by the author), these data have little value in the present paper, since it is not known whether the tendrils with a support were under tension or contact alone. WORGITZKY found in his anatomical study that marked anatomical differences come in with the grasping of a support. As to the cause of these anatomical differences, none of these investigators have written. VON DERSCHAU (**24**) by an ingenious method sought to separate the influence of tension from that of contact in his experiments with petiole twiners, by attaching a clamp to the leaf and suspending a weight thereon. Contact alone was secured by allowing a petiole merely to twine around a stick. It was found that contact alone or tension alone, gradually increased, called forth a greater development of mechanical tissue, a still greater increase taking place with the combination of both factors. It seems doubtful, however, whether the contact stimulus was avoided by this method of experimentation.

Methods

Experiments were conducted in the greenhouse under very constant and favorable conditions for growth.

Special care was taken to secure proper controls, since among tendrils, as throughout the plant kingdom, much variation occurs in size and vigor of individuals; however, it was found upon investigation that tendrils on the same vigorous vine within two or three internodes do not vary to an appreciable amount; this conclusion was based upon a comparison, by means of camera drawings, of sections of the ring of mechanical tissue of several tendrils on the same vine and on different vines, all under the same conditions (a weight of 15 grams) and all of the same size and vigor. These drawings show the areas of mechanical tissue of tendrils near each other on the same vine to coincide practically,

while those from different vines have different areas. The reliability of this method of securing controls is also shown by a comparison of the breaking strength of tendrils from the same and from different vines, which shows tendrils on the same vine under the same conditions to correspond quite closely in tensile strength.

Measurements were also taken to secure proper controls, but it was found that healthy tendrils on the same vine varied only slightly in rate of growth, and were ready for contact at approximately the same age. As the time when the tendril is most suitable for contact can be judged within 24 hours, and since the time between the maturing of tendrils on successive nodes is quite constant, a very uniform method of starting the experiment on each tendril was obtained. Moreover, when tension was applied, a certain scheme for weighting was used, to secure gradually increased tension at the same rate in each case. The experiment on each tendril was closed at exactly the same length of time from the date when it was begun, and note of weather conditions was taken during the time of experiment.

Tendrils which had been under experiment were compared by two methods: (1) by their breaking strength, and (2) by their anatomical structure. The breaking strength was obtained by wrapping the extremities of the portion to be tested with damp cotton dipped in plaster of Paris; each end was then fastened between a pair of wooden blocks, made for the purpose, which were screwed tightly together; this preparation was then placed on a machine for breaking; one of the blocks was connected to a rod on which a thumbscrew was turned, to secure gradually increasing tension; the other block was connected to a spring balance from which was read the degree of tension at which the tendril broke. A straight portion of the tendril was always taken for testing. When the break occurred at the place of attachment of the tendril, the result was thrown out.

Cross-sections of tendrils were made and microphotographs taken at a magnification of 100 diameters. This shows well the form and arrangement of the mechanical tissues. Camera sketches of the area of mechanical tissue were also made and compared with microphotographs of the same tendrils in the study of the cross-

sections. Thickness of walls was also measured with the camera lucida, and special note was taken in the anatomical study of the number and size of cells in the ring of mechanical tissue.

Tendrils were placed under tension of different degrees by causing a tendril to coil about a short piece of reed supported at either end by a wire, to which was attached a cord and the same run over a pulley, the weight desired being attached to the other end of the cord. Contact without tension was obtained by the use of a counter-balance. Unless otherwise stated, tension and contact were always secured by this means.

When a ligature was used to secure tension, a strip of soft cotton flannel was wrapped about the tendril, and the string secured by a series of hitches only tight enough to grip the tendril firmly. This was found not to injure the tendril in the least, since it develops a soft cushion of tissue at the place of contact; moreover, in *Passiflora* a greater number of xylem cells is always produced at the place of contact, which tends to prevent any injury to the tissues. Sections taken at the place of ligaturing, except where too heavy weighting was introduced, showed the mechanical tissues to be normal, and the outside diameter often greater at this place than either immediately above or below.

A series of experiments was set up to determine the effect of ligaturing on the development of mechanical tissues. Two sets of *Passiflora* tendrils were used for comparison; in the one set attachment was secured by allowing the tendril to coil about a support as already described, in the other a ligature was tied about the contact portion of the tendril, and the same amount of tension was applied to each. Breaking strengths of these tendrils are given in table I.

These results show a slightly greater average breaking strength in the ligatured tendrils over those coiled about a support; this increase is evidently due to individual variation. These experiments and observations on ligaturing show clearly that the tendril suffers no injury whatever from this treatment. When ligatures were used to eliminate the contact stimulus, they were applied in some experiments one day, in others two days after the time when the tendrils were most sensitive to contact. Carnoy's fluid (4)

was used for killing and fixing material, as this preparation penetrates woody tissues very rapidly. Sections were stained in

TABLE I

DURATION OF EXPERIMENT 32 DAYS; FINAL WEIGHT USED 20 GRAMS

	With support	With ligature
1	1050 grams	1200 grams
2	1050	975 1265
3	1275	1475
4	1350	1250
5	1425	1475
6	750	775 925
7	820	925
Average	1103 grams	1140.5 grams

anilin safranin in order to bring out clearly the lignified tissues. Permanent slides were made by mounting in Canada balsam.

Further detailed methods are given in each experiment.

Experimental work

DETAILS OF EXPERIMENTS

1. *Tendril free, with contact, with contact and tension.*—In the first series of experiments, tendrils were placed under the following three conditions: (1) without any contact whatever, (2) with contact alone, and (3) with contact and tension. In the last case, contact was secured by allowing the tendril to twine about a support as before described. The three tendrils of each set to be compared were chosen from the same vine according to the methods previously given. A final weight of 20 grams was chosen after a few preliminary trials, which showed that 20 grams was the highest weight which could be used on the average *Passiflora* tendril without producing a weakening effect. The breaking strength of these tendrils is given in table II.

These results show clearly an increase in breaking strength due to contact, and a still greater increase when tension is applied. We have yet to determine, however, whether this increase with tension is due to the longitudinal pull or to increased contact,

that is, to the increased radial pressure of the contact portion against the support, due to the pull of the weight.

TABLE II

DURATION OF EXPERIMENT 32 DAYS*

Free	Contact	Contact and tension (20 grams)
I_1—112 grams	I_2— 775 grams	I_3—1425 grams
G_1—150	G_2— 725	G_3—1170
E_1—125	E_2— 850	E_4—1050
	E_3— 675	
F_1—450	F_3—1040	F_4—1275
H_1—740	H_2—1270	H_3—1350
D_1—390	D_2— 850	D_3—1095
	B_1— 900	B_2—1050
	A_2— 575	A_3—1200
K_1—120	K_2— 375	K_3— 400
M_1—152	M_3— 575	
N_1—240	N_2— 650	N_3—1275
L_1—100	L_2— 850	
	L_6— 660	
J_1— 75		
J_5—155	J_2— 450	J_3— 700
U_1—130	U_4— 970	U_3—1125
	V_1— 450	V_5—1110
W_1—185	W_2— 365	
X_1— 40	X_2— 575	
C_1—190		
C_2—110	C_4— 408	C_5— 905
C_3—145		
P_2—100	P_1— 760	
	R_2— 580	R_1— 705
O_1— 85	O_2— 420	
	O_7— 390	O_8— 660
	Q_1— 305	
	Q_7— 490	Q_8— 630
Average (20 tendrils), 190	Average (26 tendrils), 651	Average (17 tendrils), 1007

* Capital letters denote vines, subscripts denote tendrils, which were numbered consecutively on the vine from below upward.

2. *Middle third.*—To determine the influence of tension alone the following method was devised. In the one set a ligature was tied at the distance of a third the length of the whole tendril from the tip, and another the same distance from the base (fig. 1). To the distal ligature tension was applied by running the cord over a pulley, and from the proximal ligature a cord ran to the stem, which was made taut, so as to relieve the basal third of the

tendril from any strain. In the other set, the distal ligature was placed the same as the corresponding one in the first set, and a second ligature placed just below this. To the distal one tension was applied, and from the proximal one a cord ran to the stem, relieving the basal two-thirds of tension. By this device we have one tendril with the middle third under tension, the other with this portion not under tension, and the factor of contact the same in both, except that the proximal ligature is in a more sensitive part of the tendril in the second preparation than in the first, which would tend toward a greater development of mechanical tissue in the second preparation.

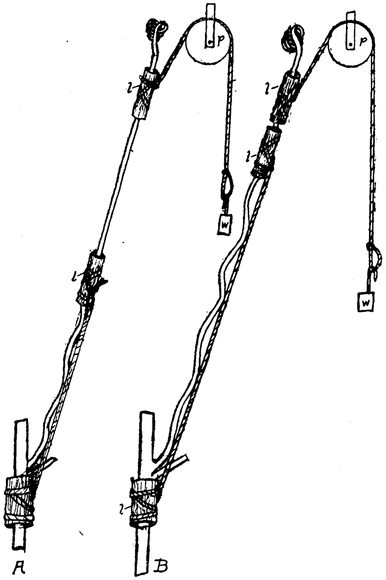

FIG. 1.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights.

Breaking strengths of the middle third of these tendrils are given in table III.

TABLE III

PERIOD 28 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free	Under tension	Tension-free
A_4—1100 grams	A_3— 875 grams	F_4—1275 grams	F_3— 950 grams
A_6— 950	A_5— 675	F_5—1090*	F_6— 900
A_8—1000	A_7— 700†	F_7—1200	F_8— 825
B_3—1475	B_2— 875	G_1—1625	G_2—1020
[B_4— 900]*	B_5— 900	G_3—1775	G_4—1000
B_7—1090	B_6— 650	G_5—1175*	G_6—1000
B_8— 900	B_9— 890	[G_7—1300]‡	
C_2—1075	C_3— 650	G_8—1535	
C_4—1075	C_5— 575	G_9—1425	G_{10}—1315†
C_7— 975	C_6— 725	G_{11}—1650	
D_4—1200	D_3— 625	H_2—1075	H_1— 735
D_5—1875	D_6— 850	H_3—1370	H_4— 865
D_8—1085	D_7— 710	H_5—1300	H_6—1685†
F_1—1325	F_2—1100		
		Average 1239	Average 862

* Broke at ligature. † Had to be broken close to base. ‡ Tension—coiled about a support.

With but one exception (H_6), these results show uniformly a decided increase in breaking strength of those under tension. The exceptional breaking strength of this tendril is partly accounted for by the fact that the break occurred in the basal third, which has a greater development of mechanical tissues. We can only conclude from these results that tension does produce greater strength of tissues in the middle third of the tendril.

3. *Basal third.*—The next experiments were for the purpose of determining the effect of tension on the less sensitive basal or proximal third of the tendril by the same method, only one ligature being used on the one under tension, however (fig. 2), and a counter-weight (*cw*) used in the one tension-free, instead of the cord being tied back to the stem. Breaking strengths of the basal third in the two sets of the tendrils are given in table IV.

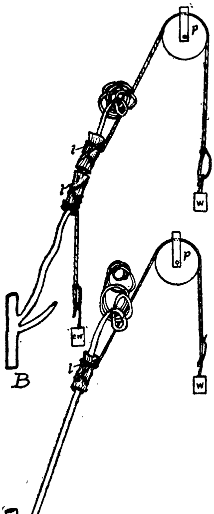

FIG. 2.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights; *cw*, counter-weight.

These results show no decided difference in strength between the two sets of tendrils compared as in the preceding experiments on the middle third. However, it is quite possible that the increase in strength of the "tension-free" tendrils in this experiment compared to the last is due to the tension stimulus received by the portion between the two ligatures, this stimulus being conducted through the tissues to the basal part; the contact stimulus is also greater here, due to the *two* ligatures compared to *one* in the tension tendril.[2]

In order to eliminate these additional stimuli the following method of experimentation was devised. Two loops of cord were made about the tendril not under tension at the same distance from the base as was the

[2] A study of sections of these tendrils (see below, under anatomical study) shows that these stimuli causing the formation of more mechanical tissue are actually transferred in the manner here stated.

TABLE IV

Series I

PERIOD 66 DAYS; FINAL WEIGHT 200 GRAMS

Under tension	Tension-free
A_4—1925 grams	A_5—1125 grams
A_8— 925	A_9—1450
B_3—1675	B_4—2150
B_7—1475	B_8—1775
G_4—2125	G_5—2000
G_8—1375	G_9—1550
Average 1583	Average 1675

Series II

PERIOD 32 DAYS; FINAL WEIGHT 50 GRAMS

Under tension	Tension-free
A_6—1890	A_7—1800
B_5—1490	B_6—1775
C_4—1260	C_5—1360
D_4—1150	D_5—1500
G_6—1600	G_7—1710
I_4—1930	I_5—1690
J_3—1270	J_4—1175
Average 1513	Average 1573

Series III

PERIOD 32 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free
C_7—1290	C_6—1440
E_6— 890	E_7— 900
F_6—1125	F_7—1160
H_5—1725	H_6—2100
	H_7—1965
I_7—1650	I_6—1600
J_6—1190	J_5—1215
O_5—1100	O_4—1400
O_6—1210	O_7—1200
Q_4— 900	Q_5— 775
S_4—1420	S_5—1220
D_6—1275	D_7— 985
Average 1261	Average 1260

ligature in the one under tension; these loops were so arranged that they acted against each other (fig. 3), so that when the upper one was run over a pulley and a weight attached and a like weight hung on the one below, a pressure equal to the weight used was exerted radially upon the tendril. In order that no injury might be done to the tendril, three lengths of soft cotton twine were placed lengthwise to the tendril, so that they lay between the loops and the tendril; this served well to transmit the pressure to the surface of the tendril. In only a very few cases was the tendril injured by this means. Where such injury occurred, the tendril was thrown out of record. In both cases attachment was made to the tendril slightly below that in the preceding experiment, so that it was just within the proximal third of the tendril, to avoid the contact stimulus as much as possible, since the sensitiveness of the tendril diminishes rapidly toward the base.

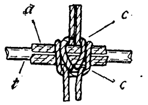

FIG. 3.—*t*, tendril; *c*, loops of cord; *a*, lengths of soft twine to protect tendril from injury.

Weights were added as in the preceding experiment. Breaking strengths of these tendrils are given in table V. Four tendrils in this series were allowed to grow without any contact whatever, to determine the effect of contact-pressure on the basal portion of the tendril, and are included in this table; likewise, one tendril which had a ligature placed similarly to those in the first two columns but without tension or contact-pressure.

These results are very different from those in the last experiment, and seem to verify the inferences made as to the real cause of the unexpected increase in strengthening tissues in the tension-free tendrils in the preceding experiments. That this increase did not take place in the "tension-free" tendrils in the experiments on the middle third is no doubt due to the fact that the part under tension in this case was in the upper or contact portion of the tendril, which is not so sensitive to the tension stimulus. "Tension-free" tendrils show an increase in breaking strength over "free" tendrils, while those under tension show a much greater tensile strength. This must mean that tension in the lower part of the tendrils is effective in giving greater strength to that portion.

Contact-pressure in this case seems to play a comparatively small part.

TABLE V

PERIOD 37 DAYS

Under tension			Tension-free			Contact-free	
Tendril	Final wt.	Breaking strength	Tendril	Final wt.	Breaking strength	Tendril	Breaking strength
A_2	100 grams	460 grams	A_1	100 grams	350 grams	A_5	115 grams
			A_4	20	190	A_6	120
C_1	100	1150	C_2	100	300		
C_4	20	1160	C_3	20	300		
C_5	20	1075	C_6	20	235	[C_7	215]*
D_2	100	975	D_1	100	325		
			D_4	20	210		
D_6	20	1385	D_5	20	275		
			D_7	20	275		
E_3	20	780	E_1	50	350		
			E_4	20	185		
			F_1	70	235		
G_1	100	1200	G_2	100	350		
G_4	20	1465					
G_5	20	111	G_3	20	210		
G_7	20	12400					
			H_2	50	225		
H_4	20	1100	H_3	20	300	H_7	160
H_5	20	925	H_6	20	190	H_8	140
Averages		1073			265		134

* This tendril had ligature only.

4. *Pressure.*—Another method of separating the influence of contact from that of tension consisted in allowing the tendril to twine about a piece of pure rubber tubing, which is very elastic, and after the coils had become firm, to apply pressure inside the tubing by means of a column of mercury. A single thickness of pure cellulose paper was wrapped about the tube to prevent any poisonous effect upon the tendril. In order that the tendril might grip the tubing tightly, so that the pressure could be applied effectively, the tubing was doubled upon itself radially and fastened by a few turns of cord; as soon as pressure was wanted, this cord was cut, which put the tendril and rubber in close contact, so that very little of the pressure from the column of mercury would be taken up by the rubber. The effectiveness of this method was aided by the contraction which takes place in the tendril after the coils have formed (FITTING 7). It was calculated that a height of

only about 10 cm. of mercury was necessary to secure the same amount of radial pressure that is exerted on the contact portion when 20 grams tension is applied to the tendril with the contact portion coiled about a support, due allowance being made for the pressure taken up by the resistance of the rubber tube.

Since, however, in spite of the care taken to secure a close contact between tendril and tube, the amount of pressure which was actually exerted upon the tendril was dependent upon how closely the tendril had coiled about the tube, only relatively high pressures were used, which were for the purpose of determining the effect of pressure alone upon the tendril. A small amount of pressure was applied at first and gradually increased. The tensile strength of the whole tendril was determined in all experiments on the effect of pressure, to see whether an actual increase in the strength of the tendril had occurred. The break occurred, with a very few exceptions, in the middle third.

TABLE VI

PERIOD 28 DAYS

Increased pressure			Normal pressure	
Tendril	Hg. height	Breaking strength	Tendril	Breaking strength
A_2	55 cm.	1085 grams	A_1	785 grams
E_4	30	1775	E_2	975
			E_3	1025
I_2	22	1150	I_1	715
I_3	30	950		
L_2	20	715	L_1	615
L_3	30	960	L_5	625
M_4	45	900	M_3	575
M_5	30	720		
M_6	30	1160		
N_3	30	915	N_5	725
N_4	30	850		
V_3	30	700	V_4	500
Averages		990		727

The breaking strengths as shown in table VI show an undoubted increase in the strength of tendrils with increased radial pressure. That the increase was small in some cases may be due to the failure of the tendril to coil about the tubing securely.

That longitudinal tension may enter into this experiment is quite possible; however, in many tendrils in this experiment where pressure was applied, the contact with the rubber tubing was so close as to permit of a seemingly small amount of longitudinal stretching. That this increase was not in the main due to longitudinal tension may be inferred by a comparison with the results in table VII.

TABLE VII

PERIOD 28 DAYS

Pressure with weight			Contact pressure	
Tendril	Final wt.	Breaking strength	Tendril	Breaking strength
H_1	15 grams	625 grams	H_2	520 grams
K_1	20	600		
K_2	15	685	K_5	740
K_4	5	775		
L_1	20	540		
L_3	20	690	L_2	650
L_4	15	875	L_5	675
M_5	20	875		
M_6	20	600	M_1	600
M_7	15	975		
N_1	20	775		
N_2	20	935	N_5	675
N_3	15	675		
S_1	20	790	S_5	575
S_2	15	890		
Averages		745		634

In order to determine how great a part pressure actually has in the formation of mechanical tissue in tendrils, weights were placed upon the most sensitive part of the tendril, the latter being supported by a small platform suspended from above by a cord. Weights were added exactly the same as when tension was used in the former experiments, and the same length of the tendril was placed under pressure as was calculated to be under pressure in the tension experiments.

The breaking strengths of these tendrils as given in table VII show a slight increase over those tendrils which had contact alone. We infer from this that the additional radial pressure caused by an amount of tension equal to 20 grams does not greatly increase

the strength of the tendril. This may be explained by the supposition that a weight of 20 grams does not exert a pressure much greater than is caused by the contraction of the contact portion of the tendril when coiled about a support.

Ligatures were also tied about tendrils in different regions to determine the effect of contact in a more and in a less sensitive part of the tendril. The effect of these ligatures in regions *a* and *b*, respectively, upon the breaking strength is shown in table VIII; *a* was about one-third the length of the whole tendril from the apex, and *b* the same distance from the base of the tendril.

TABLE VIII

PERIOD 32 DAYS

Ligature at *a*		Ligature at *b*	
Tendril	Breaking strength	Tendril	Breaking strength
B_7	230 grams	H_8	590 grams
D_8	550	H_{10}	310
D_9	510	H_{11}	160
I_5	490	K_4	140
I_6	650	K_5	225
J_2	650	K_6	260
J_4	700		
J_5	665		
L_3	510		
M_3	600		
M_4	750		
Averages	573		281

These results show that a ligature placed in a more sensitive region (*a*) calls forth a greater formation of mechanical tissue than when placed in a less sensitive region (*b*). This accords with the former inferences made in experiments on the middle third and basal third.

RESULTS IN BREAKING STRENGTH

The following conclusions may be deduced from the foregoing results in breaking strength of tendrils:

1. Contact alone plays an important part in giving strength to the tendril.

2. When contact is increased by pressure, a further increase in the strength of the tendril is produced.

3. When the factor of tension is added to that of contact, a still greater strength results to the tendril.

ANATOMICAL STUDY

1. *General anatomy of the Passiflora tendril.*—A cross-section of a tendril of *Passiflora caerulea*, in accordance with the observations of MACDOUGAL (**13**) and WORGITZKY (**26**), reveals the following tissues, beginning at the outside: epidermis, collenchyma, thin-walled parenchyma, bast, xylem (which forms a complete ring, due to secondary growth), and in the center pith. In mature tendrils the pith entirely fills the central part except in the basal portion, where there is a central cavity within the pith. The walls of the xylem and bast are much thickened, and so are (as WORGITZKY has noted, p. 34) the walls of the pith. The xylem becomes lignified, also the bast somewhat, and, as MACDOUGAL observed, lignification extends to the pith also.

At the base the arrangement of tissues is very nearly radial, but in the portion in contact a marked dorsiventrality is seen, which is due principally to the development of the xylem to a much greater extent on the side in contact. A section midway between the apex and base of the tendril shows a slight dorsiventrality, a somewhat greater amount of xylem being formed on the concave side.

2. *Study of sections; experiments on entire tendril (free, with contact alone, and with contact and tension).*—Sections were made through the middle of the tendrils, as this was found to be the place at which the break invariably occurred in these experiments. Tendrils as near as possible to the average breaking strength were taken for sectioning. A comparison of sections reveals the following.

The mechanical tissue of the free tendril is limited to a small area of xylem on the concave side, and only the four primary bundles on the opposite side. The xylem cells are quite thin-walled compared with the xylem of the other tendrils in this experiment, and the primary bundles of the opposite side are

composed of two or three slightly thickened vessels. In this region only a few bast fibers are present, which are very small; very little pith is present, which lines a central cavity. Toward the base a complete ring of thin-walled xylem and pith is formed.

Sections of those tendrils under contact and under tension show the normal complete ring of mechanical tissue and central thin-walled pith. At the first examination of these sections, little difference could be seen in structure or areas of mechanical tissue, and camera sketches show no difference in thickness of walls of the xylem, though the greater part of those under tension had a tensile strength 50 per cent higher than those with contact alone. A closer examination of the sections with the aid of microphotographs and camera sketches shows that while the xylem areas are approximately the same in both, in the one where tension had been introduced the walls of the pith cells have become much thickened, while in the one with contact alone they are quite thin-walled. This thickening of walls takes place usually throughout the whole area of the pith of the tendril under tension, while in the one which had been under contact alone the pith is thin-walled throughout. It is worthy of note also that in sectioning, the ones under tension were much harder to cut through, which is no doubt due to a difference in density of cell walls.

3. *Study of sections; experiments on middle third.*—Examination of sections of those tendrils where the middle third was (1) with and (2) without tension shows the diameter of mechanical tissue to be much greater in the latter, which accounts for the greater outside diameter usually found in these tendrils. This seemingly greater area of mechanical tissue in the tendril grasping a support but not under tension is somewhat surprising when we consider that those under tension had a breaking strength nearly 50 per cent higher. This increased strength with tension is at least partly accounted for by the fact that the pith walls in the tension-tendril are thickened (very similarly to those in the preceding experiment under tension), while in the one not under tension all the pith is thin-walled. In order to be certain that this thickening of the pith is constant with those under tension, sections of more than 30 tendrils in this experiment were studied

and compared, each being labeled so that it could not be told during the examination which was from a tension and which from a tension-free tendril. In every case it was possible to decide with certainty which one had been under tension from the appearance of the pith, and each decision was later verified by referring to the record. The walls of the pith were in most cases thickened in a marked manner to the very center. Measurements with a planimeter show the tension-free tendril to have the greater area of xylem, while the tension-tendril has the greater amount of mechanical tissue when thick-walled pith is included. Comparative areas were found to be as follows:

	Xylem	Pith (thick-walled)	Total
Under tension	2.61	2.78	5.39
Tension-free	4.51	....	4.51

In these experiments, as in the others where tension was used, a marked characteristic of the sections of tension-free tendrils was that the pith was found more or less displaced by the process of sectioning, while in those from tension-tendrils the pith held its shape as if firm.

In all these tendrils it was noted that tendrils which had been under tension were more rigid and much harder to cut through than those free of tension, as noted in the preceding experiments.

Sections were taken also through the basal third of these same tendrils. A close resemblance was found between sections in these two regions (middle and base) in the same tendril. In the basal part of the tendril in which the middle third had been under tension, the diameter of the mechanical tissue is smaller and the pith thick-walled throughout, while in the tendril tension-free the pith is very thin-walled in the corresponding region. This shows remarkably how the stimulus for growth may be transferred through the tissues to a part which has not received the stimulus directly, since the basal part in neither case in these experiments was under tension.

4. *Study of sections; experiments on basal third.*—Sections of tendrils in which the basal third was tested were studied with the

view especially to ascertaining the cause of the difference in results obtained in breaking strength under the two different methods of experimentation (see tables IV and V). Sections of tendrils in the first set of experiments (where two ligatures were used in the one not under tension) showed the ring of mechanical tissue in the one not under tension to have a greater outside diameter than that in the one under tension. Xylem and thickened pith are present in both tension and tension-free tendrils. A well marked difference could be observed, however, between the amounts of xylem and thickened pith in the two sets of tendrils. In the one not under tension xylem was present in greater quantity than in the one which had been under tension, while in the tension-tendril thickened pith was in much greater quantity than in the one without tension. In a typical tendril the comparative amounts of xylem and thick-walled pith were as follows:

	Xylem	Pith thick-walled	Pith thin-walled	Total mechanical tissue
Under tension.	6.0	4.7	(1.7)	10.7
Tension-free.	7.2	1.8	(3.6)	9.0

The fact that, nothwithstanding the smaller area of mechanical tissue, the breaking strength of the ones not under tension was practically the same as in those under tension, is no doubt due to the fact that much of the thick-walled pith in the tension-tendril does not possess as thick walls as does the xylem; hence does not give as much strength to the tendril as does the latter. An examination of sections in the second series of experiments on the basal third, where contact-pressure was applied to the tension-free tendril by means of two loops of cord pulling against each other, shows a very different appearance from that just described when tension and tension-free tendrils are compared. In this case the area of xylem is practically the same in both, being about equal to the amount found in those under tension in the above experiments on the basal third; in the ones not under tension the pith is thin-walled throughout, is small in amount, and has a large cavity in the center; in the ones under tension the pith is much

thickened, is larger in amount than in the last, and the central cavity is much smaller.

If we now compare the structure of the tendrils in the two methods of experimentation, it becomes very evident that the additional amount of xylem in the tension-free tendrils (as compared to the tension-tendrils) of the first set is due to the extra contact-pressure introduced, and the thick-walled pith found in the same tendrils, which has not before appeared in tendrils except when tension was introduced, is due to the stimulus of tension conducted to the basal part from the portion in tension between the two ligatures. That this thickening of the pith which was caused by only a small portion of the tendril being under tension did not appear in the former experiments on the middle third of the tendril is no doubt due to the fact that the tension in the latter case was in the contact portion of the tendril, which is not so sensitive to the stimulus of tension as is the lower two-thirds of the tendril.

5. *Study of sections; experiments on contact portion.*—Examination of sections through the contact region of tendrils which had been put under (comparatively) great pressure by a column of mercury failed to detect any difference in anatomical structure when compared with those which had been in contact only. Sections through the middle of the tendrils, however, where there was no tension and where the break usually occurred, show marked differences between the two sets of tendrils in the amount of xylem present. The area of xylem in the ones which had been under pressure, in an average tendril, was approximately twice as great as the area of xylem in the ones which had been in contact only. No differences in the pith could be detected; it was thin-walled alike in both sets of tendrils.

In those cases where a pressure of 20 grams was obtained by laying a weight on the tendril, no difference could be observed between these tendrils and those under mere contact, though the former had a slightly greater average breaking strength. Both had the usual ring of xylem and the pith was thin-walled.

Sections were not made of tendrils which were ligatured in different regions.

SUMMARY AND CONCLUSIONS

These changes in structure under changing conditions which were observed upon a number of tendrils in each condition and were found constant in each case, almost without exception, have but one meaning to the writer. In experiments where tension was introduced, the marked increase in thickness of pith walls, which was found only when the factor of tension was present, can be explained only by the theory that this thickening is due to the longitudinal pull on the tendril, by which the tensile strength of the tendril is increased.

That pith may serve as mechanical tissue is a thing for which no evidence has heretofore been offered. DEBARY says (*Comp. anat.*, p. 533):

> The only demonstrable change in the pith during the phenomena of secondary growth is that it sooner or later, rapidly or slowly, dies off and dries up. The possibility of a change in the pith caused directly by the growth in thickness is not, indeed, excluded a priori. For . . . . the increasing pressure . . . . exercised on the pith [by the xylem] may lead to anatomical changes in the latter. In what cases and in what form such changes may possibly take place are questions which have not been investigated, and to the solution of which there is scarcely any safe clue; the possibilities will not be discussed here.

WORGITZKY noted a thickening of the walls of the pith in the tendrils of *Passiflora caerulea*, *P. triloba*, and *P. quadrangularis*, "after a support had been securely grasped." He also adds "the purpose or cause of this was not found"; and MACDOUGAL noted that lignification extended to the pith in the basal part of tendrils of *P. caerulea*.

In view of the results of observations and experiments presented in this paper, I maintain that this thickening of the walls of the pith cells in *Passiflora caerulea* is an adaptation, where tension acts as an irritation-stimulus, for producing greater tensile strength to the tendril where needed.

In the series of experiments on the contact portion, the great increase in xylem below the part in contact, accompanying the increased pressure, leads to the conclusion that contact-pressure has a marked effect upon the structure of the tendril. That a pressure of 20 grams does not cause a decided increase in xylem

may be explained if we assume that the pressure exerted on the support by the coils of the part in contact which contract after grasping the support is equal to 20 grams for the whole area in contact. No constant change could be noted in the amount of bast present under these varying conditions, except that very little could be found in the free tendrils. As the bast plays only a comparatively small part in the *Passiflora* tendril, this tissue was not taken into consideration.

The conclusion from these anatomical studies on *Passiflora* can only be that contact-pressure causes a greater formation of xylem in the tendril, while longitudinal tension causes a thickening of the walls of the pith whereby greater tensile strength is secured.

General conclusions

To return to the problem of the present paper (as given in the introduction), my conclusion in regard to *Passiflora caerulea* is that those tendrils which function to support the plant, that is, that are under the influence of contact and tension, possess a greater breaking strength than those which have grasped no support (see table I).

The cause of this greatly increased strength, as shown by the experiments on the middle third, basal third, and contact portion, and a study of sections of the same, is clearly due to a combination of the two factors contact and tension, the cells of the xylem being increased both in number and in thickness of walls by the former stimulus, and the walls of the pith much thickened by the latter. Comparing the values of these two factors in the formation of mechanical tissue in the *Passiflora* tendril, I conclude that contact plays by far the most important part, though the strength of the tendril may be still more increased (even 50 per cent) by the additional factor of tension.

As to the influence of contact upon the formation of tissues, we have had a large number of observations, not only in regard to tendrils, but also in regard to plant tissues in general.

That tension also may act as a stimulus, and that thereby stronger tissues are built up in the plant, has been shown by the experiments of BORDNER (**3**); this is substantiated by the observa-

tions and experiments presented in this paper. This accords with the observations of HEGLER (**8**) that the retarding effect of tension is closely related to the daily periodicity of growth in length, which seems to show that tension acts as a true stimulus upon the plant cell. As to the exact method by which this increase and strengthening of tissue takes place we are unable to say, since we know very little, as yet, of the nature of the changes taking place in the cell and especially in the cell wall, under the influence of tension.

It seems not unlikely that this increased growth is due to increased hydrostatic pressure in the cell, since HEGLER found a higher hydrostatic pressure in plants which had been under tension than in plants growing normally (**7**, p. 416).

The state of tension in which the cell wall might be, may act as an irritation-stimulus for the laying down of more tissues either by apposition or intussusception; here, however, we should have to assume the cell membrane (at least in part) to be composed of living protoplasm, for which assumption we have no well founded evidence (see PFEFFER **18** [EWART transl.], **1**:485).

As to why this thickening in *Passiflora* did not occur in the xylem also under the influence of tension, we are unable to say; this difference in response is probably due to fundamental differences in these tissues.

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